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RESEARCH ARTICLE

"Targeting or Supporting, What Drives Patterns of Aggressive Intervention in Fights?"

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GrooFiWorld is an individual-based, computational model of social interactions that can be used to examine factors underlying reciprocation and interchange of social behavior in primate societies. Individuals within GrooFiWorld are programed to maintain spatial proximity and thereby form a group. When an individual encounters another individual in its proximity, the individual attacks the other if the risk of losing is low. Otherwise, the individual considers grooming the other. Patterns of social behavior that emerge in the model resemble empirical data from primates. Triadic aggression emerges when an individual attacks one of the former combatants by chance immediately after an aggressive interaction, and reciprocation and interchange of grooming and support emerge even though individuals have no intention to help others or pay back services. The model generates predictions for patterns of contra-intervention that are counterintuitive within a framework of interchange of social services, such as that individuals receive more contra-intervention from those whom they groom more frequently. Here we tested these predictions in data collected on social interactions in a group of bonnet macaques (*Macaca radiata*). We confirmed the predictions of the model in the sense that contra-intervention was strongly correlated with dyadic aggression which suggests that contra-intervention is a subset of dyadic aggression. Adult females directed more contra-intervention to those individuals from whom they received more grooming. Further, contra-intervention was directed down the dominance hierarchy such that adult females received more contra-intervention from higher ranking females. Because these findings are consistent with the predictions from the GrooFiWorld model, they suggest that the distribution of interventions in fights is regulated by factors such as dominance rank and spatial structure rather than a motivation to help others and interchange social services. Am. J. Primatol. 78:247–255, 2016.

Key words: individual-based models; bonnet macaques; interchange; contra-intervention; grooming

INTRODUCTION

Coalitionary aggression is a common type of behavior in primate societies [Harcourt & de Waal, 1992]. It occurs when an individual intervenes aggressively during or immediately after a fight between two opponents and helps one against the other. Thus, aggressive interventions are pro someone (i.e. pro-intervention or support) and contra someone (i.e. contra-intervention) [de Waal & Luttrell, 1988]. Aggressive interventions are usually considered altruistic because interveners suffer the risk of injury by helping one of the opponents (the aggressor or the victim) against the other. Hence, it is thought that interveners should receive a benefit in return from the recipient of pro-intervention or support [Trivers, 1971]. Therefore, empirical studies have usually focused on the relationship between the intervening individual and the one receiving support. These studies have indeed found that individuals usually reciprocate support and/or interchange it for grooming and vice versa [Hemelrijk & Ek, 1991; Hemelrijk et al., 1999; Schino, 2007; Schino

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et al., 2007; Watts, 2002]. Few studies, however, have focused on the opposite relationship, the one between the intervening individual and the one it aggresses, (i.e. the recipient of contra-intervention). In this case, the intervening individual opposes or directs an act of contra-intervention to one of the opponents of the fight [de Waal & Luttrell, 1988; Hemelrijk & Ek, 1991; Silk, 1992]. Hence, we define an act of contra-intervention when a bystander intervenes in a conflict between two individuals by aggressing one of the opponents, because herewith it directs an act of contra-intervention to that opponent. In the present study, we analyzed patterns of contra-intervention in a group of bonnet macaques (*Macaca radiatta*). Our aim is to test predictions that have been derived from a computational model called "GrooFiWorld" [Hemelrijk & Puga-Gonzalez, 2012].

GrooFiWorld is a spatially explicit individual-based model. This model reproduces patterns of reciprocation and interchange of grooming for support like those described in tolerant and intolerant primate societies [Hemelrijk & Puga-Gonzalez, 2012]. In the model these patterns emerge as a side effect of rank and/or the socio-spatial structure of the group. This suggests that a similar mechanism may regulate aggressive interventions in primate societies. The model, however, is unable to exclude the possibility that other cognitively higher mechanisms such as "calculated reciprocity" or "emotional bookkeeping" may underlie reciprocation and interchange of grooming and support in primates [de Waal & Brosnan, 2006; Schino & Aureli, 2009]. Nevertheless, the model delivers predictions, regarding patterns of contra-intervention, which seem counterintuitive with "calculated reciprocity" or "emotional bookkeeping." Thus, to distinguish between the mechanisms suggested by the model and other cognitive mechanisms; in this study, we tested the predictions of the model in empirical data of a group of bonnet macaques.

In GrooFiWorld individuals interact with others in their proximity by fighting or grooming them according to simple behavioral rules (for a brief description of the model see supporting information). In the model there are no separate rules for coalitions. However, coalitionary aggressive interventions are observed when after an aggressive interaction a nearby individual attacks one of the former combatants. For example, when *C*, being close to the former combatants *A* and *B*, attacks *B*. This is counted as an act of support of *C* for *A*, and an act of contra-intervention of *C* against *B*; just as it is done when recording coalitionary behavior of primates [de Waal & Luttrell, 1988; Hemelrijk & Ek, 1991; Hemelrijk & Puga-Gonzalez, 2012].

In the model, patterns of support and contra-intervention emerge due to the socio-spatial structure of the group. A socio-spatial structure with dominant individuals in the center of the group emerges because subordinates regularly avoid dominants while still trying to stay in the group [Hemelrijk, 1999, 2000]. This structure influences the distribution of social interactions because individuals interact most often with others in close proximity. Rank influences the distribution of social interactions especially when the dominance hierarchy is steep. This is a consequence of the risk-sensitive behavior individuals follow when attacking another [Hemelrijk, 1999; see also supporting information]. When the dominance hierarchy is steep, the risk of losing a fight from a dominant individual is high. Therefore, subordinate individuals refrain from attacking higher ranking individuals and groom them instead. This results in grooming being directed up the hierarchy. Further, high ranking individuals intervene more often in fights because they experience low risk when attacking others. Thus, they are also the main providers of support and contra-intervention [Hemelrijk & Puga-Gonzalez, 2012]. This leads to the emergence of positive correlations between grooming given, support received, and receipt of aggression at the group level. Thus, in the model individuals statistically interchange not only grooming for receipt of support but also grooming for receipt of aggression (both dyadic aggression and contra-intervention). Further, the distribution of contra-intervention and dyadic aggression is positively associated (i.e. individuals directed contra-intervention more often those group members they attack more frequently). The close association of contra-intervention and dyadic aggression is not surprising because contra-intervention is a subset of dyadic aggression due to the lack of coalitionary rules in the model. Thus, the distribution of contra-intervention is also regulated by rank and spatial structure of the group.

We tested six predictions from the model in the female bonnet macaques. First we tested whether contra-intervention and aggression were positively correlated: (i) whether females directed contra-intervention more often those other females that they attacked more often during dyadic fights and (ii) whether they received contra-intervention more often from those females from whom they received attacks more often during dyadic fights. Then we tested the interchange of grooming for aggression: (iii) whether females directed contra-intervention or (iv) attacked in a dyadic fight more often those females by whom they were groomed more frequently, and (v) whether they received more contra-intervention or (vi) dyadic attacks from those females that they actively groomed more often [Hemelrijk & Puga-Gonzalez, 2012].

To test these predictions, we used data on aggression, grooming, support, and contra-intervention from a group of bonnet macaques. Bonnet macaques live in a matrilineal society with multi-male, multi-female groups in which coalitionary

aggression is common [Kumara et al., 2010; Silk, 1982; Thierry, 2000]. Macaque species are usually classified according to dominance style which varies from extremely intolerant to extremely tolerant also referred to as ranging from grade 1 to grade 4. Bonnet macaques are classified as mildly tolerant (grade 3) [Thierry et al., 2004]. We investigated whether patterns of contra-intervention in female bonnet macaques were consistent with predictions derived from the GrooFiWorld model. Furthermore, we also investigated whether in this group females reciprocated and interchanged grooming for support, and whether the patterns of social interaction were consistent with a mildly tolerant dominance style [Thierry et al., 2004].

TABLE I. Group Composition, Counter Aggression, and Acts of Grooming, Aggression, Support, and Opposition in the Group of Bonnet Macaques

Number of individuals present during the whole period:	
Males	8
Females	13
Juveniles	21
% of counter aggression (absolute frequency of aggression)	
All	15 (918)
Males	20 (186)
Females	4 (345)
Total acts between two adult females in the matrix of:	
Grooming	2,378
Aggression	342
Support	76
Opposition	80

METHODS

Ethical Standards

All animal procedures were approved by the University of Georgia Institutional Animal Care and Use Committee and were in compliance with Indian Law. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates.

Subjects and Living Conditions of Study Groups

We collected behavioral data on a group of bonnet macaques (*M. radiata*) living at Chamundi Temple located near Mysore, India. Details of this study groups and our data collection procedure have been published elsewhere [Cooper et al., 2004, 2007]. The animals moved freely around the temple site and nearby houses as well as on the surrounding hills. The bonnet macaques received food each day at irregular times from humans at a variety of locations near the temple and foraged on natural vegetation. During the study period, group size fluctuated from 41 to 49 animals due to migration and emigration. Group composition of animals present throughout the study and their age–sex distribution are shown in Table I.

Behavioral Observations

Data collection was completed over a 12 months period (from November 1999 to October 2000) with 907 hr of total observation. Data collection began after inter-observer reliability reached more than 90% agreement on focal samples.

Focal animal sampling was conducted on all adult animals as well as several subadult males. Ten hours per individual of focal sampling were collected. During focal samples, all affiliative and agonistic interactions involving the subject as well as the identity of the initiator and recipient were recorded. Affiliative behavior included allogroom, embrace, contact (including manual touch, passive touch, and huddle), play, muzzle touch, lip-smack, genital touch, and mount. Agonistic behavior included silent bared-teeth display, lip-grin, avoid, flee, open-mouth threat, swing, lunge, charge, chase, manual contact aggression, bite, and severe bite. Our ethogram was derived from previous research on macaques [Bertrand, 1969; de Waal & Luttrell, 1989; Petit & Thierry, 1992]. All agonistic responses involving a third-party were recorded indicating the direction of support. Before the start of each focal sample, the identity of each adult and subadult individual in view and its distance from the focal subject was recorded. Distances were defined as <5 m, 5–25 m, and >25 m. The occurrence and direction of agonistic behavior and grooming were also recorded ad libitum. Ad libitum data included adults, sub-adults, and juveniles. The number of acts of grooming, aggression, support, and contra-intervention are shown in Table I. Note that the sample size of acts of support is different from that of acts of contra-intervention because only the acts of contra-intervention or support between two adult females were used in the analysis.

We combined data from focal animal sampling and ad libitum sampling to construct matrices of the direction of behavior. The inclusion of ad libitum data is appropriate because visibility does not alter the direction of behavior. Focal sample data were added to the ad libitum data in order to increase the number of interactions in each matrix. We constructed directional matrices for the following activities: grooming, aggression, counter aggression, submission, support, and contra-intervention. Further, a visibility matrix was constructed from the data of individuals-in-view at the start of each focal sample. This matrix was used to correct for opportunity to support or contra-intervention (see statistical analysis). Also, a symmetrical proximity matrix was constructed from scans of the distance between the

focal subjects and each group-member at the beginning of each focal sample. The data in this matrix indicated the number of scans in which animals were within 5 m of each other. Dominance hierarchies were constructed from the direction of all submissive interactions including silent bared-teeth display, avoid, and flee. We defined counter aggression as events in which the recipient of aggression responded immediately to the original aggressor with any form of aggressive behavior (e.g. open-mouth threat, swing, lunge, charge, chase, manual contact aggression, bite, and severe bite).

Statistical Analysis

This study focused on female–female interactions because of the importance of female social relationships in matrilineal macaque societies. Therefore the predictions of GrooFiWorld focus on adult females relationships only. In order to test for reciprocation and interchange, matrix correlations were computed by means of the Tau-Kr correlation as described by Hemelrijk [1990a]. According to this method, reciprocity and interchange occurs when each individual directs more often acts to those partners from whom it receives more frequently acts in return. The TauKr test involves correlations between the rows of two matrices by means of Kendall's statistic of which values are summed over all rows [Hemelrijk, 1990a]. The probability of the observed value is calculated using Mantel's permutation procedure [Mantel, 1967]. The level of significance was calculated using 2,000 permutations. We chose this method, instead of general linear mixed models (GLMM), because it controls for the recurrence of individuals. We tested for reciprocity and interchange of social behaviors by correlating a matrix of giving acts with one comprising data on receipt of acts. We also tested whether social behavior was correlated with proximity or the dominance rank of the interaction partner. To do so, the matrix of giving (or receiving) acts was correlated with the matrix of proximity or with the matrix of dominance rank of the partner. In the matrix of rank of the partner individuals that were more dominant were represented with a higher number. All correlations were controlled for rank and proximity by means of the partial TauKr correlation [Hemelrijk, 1990b]. We excluded rows that include only zeros in both matrices. Because we were testing predictions of the model, all tests are one-tailed.

Matrices of support were corrected for opportunity to support. Presumably, opportunities to support are the total number of agonistic interactions an individual is involved and thus can be supported by another. However, opportunities to support another depend on individuals being in visual proximity during an agonistic interaction. Hence, we first calculated the proportion of agonistic interactions in which a dyad of individuals may have been in visual proximity to other group members. To do so, we created a symmetrical matrix of visibility, that is, proportion of focal samples in which a dyad of individuals was in visual proximity to others. Then, we created an opportunity matrix by multiplying the symmetrical matrix of visibility by the symmetrical matrix of total agonistic interactions. Finally, matrices of support were corrected for opportunity by dividing them by the opportunity matrix. The same was done to correct the matrix of contra-intervention for opportunity. To increase sample size and thus the power of the statistical analysis, we included all coalitions in which at least two of the participants were adult females disregarding whether the target or beneficiary was a subadult or a juvenile individual (Table I).

RESULTS

Predictions of the Model

We confirmed the six model-based predictions in the group of bonnet macaques (Table II). We found that contra-intervention was positively correlated with dyadic aggression. Adult females directed more contra-intervention to those adult females to whom they also directed more dyadic aggression, and adult females received more contra-intervention from those adult females from whom they also received more dyadic aggression (1–2 in Table II). Further, active grooming was positively correlated with the receipt of dyadic aggression and of contra-intervention. Adult females directed more grooming to those individuals from whom they received more dyadic aggression and from whom they received more contra-intervention (3–4 in Table II). In addition, dyadic aggression and contra-intervention were also positively correlated with the receipt of grooming. Adult females directed both more dyadic aggression

TABLE II. Testing Predictions on Aggression and Opposition in Adult Female Bonnet Macaques Studied with Matrix TauKr Correlations

TauKr matrix correlations between	TauKr (*P*-value)
(1) Opposition given and aggression given	0.59 (0.000)
(2) Received opposition and received aggression	0.53 (0.000)
(3) Received aggression and grooming given	0.20 (0.002)
(4) Received opposition and grooming given	0.28 (0.000)
(5) Aggression given and received grooming	0.28 (0.000)
(6) Opposition given and received grooming	0.33 (0.000)

The TauKr coefficients and *P*-values are shown.

and more contra-intervention to those from whom they received more grooming (5–6 in Table II).

Reciprocation, Interchange, and Dominant Style

Female bonnet macaques reciprocated grooming but not support (1–2 in Table III). Further, we found a trend ($P = 0.076$) for the correlation between grooming given and support received. Adult females appeared to direct more grooming to those females from whom they received more support (3 in Table III). However, the correlation between support given and grooming received was not significant. Adult females did not direct more support to those adult females from whom they received more grooming (4 in Table III).

In our group of bonnet macaques adult females exhibited traits of an intolerant dominance style: grooming was directed up the dominance hierarchy, and aggression and contra-intervention were unidirectional (5–7 in Table III). Further, females showed a low proportion of counter-aggression in their agonistic encounters (4%, Table I), which is similar to the percentage found among macaque species with an intolerant dominant style [Cooper & Bernstein, 2008].

Correlations With Dominance Rank

Dominance rank was correlated with grooming given but not with grooming received (1–2 in Table IV). Adult females directed more grooming toward higher ranking partners. Further, dominance rank was also correlated with aggression and contra-intervention. Adult females directed less aggression and contra-intervention toward higher ranking females (5–6 in Table IV); and received more aggression and contra-intervention from higher ranking females (7–8 in Table IV). Support was not correlated with rank (3–4 in Table IV).

TABLE IV. Matrix Correlations Between Grooming, Support, Opposition, Aggression, and Rank of the Partner Among Female Bonnet Macaques

Matrix correlation between rank of the partner and:	TauKr (*P*-value)
(1) Grooming given	0.22 (0.011)
(2) Grooming received	−0.13 (0.102)
(3) Support received	0.10 (0.068)
(4) Support given	0.06 (0.262)
(5) Aggression given	−0.39 (0.001)
(6) Opposition given	−0.19 (0.041)
(7) Aggression received	0.26 (0.009)
(8) Opposition received	0.18 (0.020)

In the matrix rank of the partner, the rank of dominant individuals is represented by a high number. The TauKr coefficients and *P*-values are shown.

Correlations With Spatial Proximity

Spatial proximity was positively correlated with grooming given and received (1–2 in Table V). Dyads of females that groom the most were usually closer in spatial proximity. None of the other social behaviors was correlated with proximity (3–8 in Table V).

DISCUSSION

In this group of female bonnet macaques, the patterns of contra-intervention, dyadic aggression, and grooming were consistent with the predictions of the model GrooFiWorld. Females attacked more often those to whom they directed contra-intervention more frequently; they received more often attacks from those from whom they received more frequently contra-intervention; and they interchanged grooming for receipt of contra-intervention. In the model, these patterns emerge due to the socio-spatial structure of the group, the risk-sensitivity of attack, and the fact that grooming is

TABLE III. Reciprocation, Interchange, and Dominant Style in Adult Female Bonnet Macaques Studied with Matrix TauKr Correlations

Reciprocation and interchange:	TauKr (*P*-value)
(1) Grooming given and its receipt	0.23 (0.002)
(2) Support given and its receipt	0.05 (0.258)
(3) Grooming given and received support	0.10 (0.076)
(4) Support given and received grooming	0.08 (0.140)
Patterns of dominant style:	
(5) Grooming given and rank of the partner	0.22 (0.011)
(6) Aggression given and its receipt	−0.41 (0.000)
(7) Opposition given and its receipt	−0.24 (0.008)

The TauKr coefficients and *P*-values are shown.

TABLE V. Matrix Correlations Between Grooming, Support, Opposition, Aggression, and Proximity Among Female Bonnet Macaques

Matrix correlation between proximity and:	TauKr (*P*-value)
(1) Grooming given	0.35 (0.000)
(2) Grooming received	0.16 (0.025)
(3) Support received	0.01 (0.414)
(4) Support given	−0.03 (0.652)
(5) Opposition given	0.00 (0.486)
(6) Opposition received	0.04 (0.320)
(7) Aggression given	−0.08 (0.830)
(8) Aggression received	0.11 (0.083)

The TauKr coefficients and *P*-values are shown.

more likely if an individual estimates it will lose a fight [Hemelrijk & Puga-Gonzalez, 2012].

In our group of bonnet macaques patterns of social behavior also emerge due to rank effects and to spatial proximity. Females directed grooming more often to higher ranking females (Table IV) and to females in closer proximity (Table V). Females directed more aggression and contra-intervention to others the lower the rank of others; and the higher the rank of females the less often they received aggression and contra-intervention from others (Table IV). Thus individuals directed more often grooming to those from whom they received more often aggression and vice versa. After partialling out dominance rank, correlations between grooming and contra-intervention became weaker but remained significant (Table VI). This finding suggests that there is another unknown variable giving rise to these patterns. Alternatively, as we have previously shown [Hemelrijk & Puga-Gonzalez, 2012], the partial Tau-Kr statistic may fail to completely remove the effects of dominance rank (see below).

Proximity was correlated with grooming but neither with aggression nor with contra-intervention (Table V). This may be due to the small sample size of our scans, the low frequency of aggression, and because individuals will seldom attack higher ranking animals.

Consistent with our results, there are at least other four studies that have found a correlation between grooming and aggression. In Japanese macaques (*Macaca fuscata*) and wild white-faced capuchin monkeys (*Cebus capucinus*), females directed more grooming to those partners from whom they received more aggression [Perry, 1996; Schino et al., 2005]. In Barbary macaques (*Macaca sylvanus*) females attacked more often those females from whom they received grooming more often [Carne et al., 2011]. Similarly, in stumptail macaques (*Macaca arctoides*), adult males directed more grooming to those from whom they received more aggression [Richter et al., 2009]. This kind of behavioral pattern is usually interpreted as appeasement of dominant individuals [Carne et al., 2011; Schino et al., 2005]. Our study does not address whether grooming has an appeasement function, it merely indicates that the distribution of aggression, contra-intervention, and grooming may be regulated by dominance rank and social spatial structure.

Proximity and rank [c.f. symmetry-based reciprocity Brosnan & de Waal, 2006] have already been considered as possible mechanism underlying patterns of reciprocation and interchange of grooming and support in primates. However, researchers have concluded that these variables are not the causal factor because matrix correlations between acts given and received remain significant after partialling them out [de Waal & Luttrell, 1988; Gomes & Boesch, 2009; Hemelrijk & Ek, 1991]. Interestingly, our model has shown that partial correlations are not sufficient to eliminate the effects of rank and/or proximity. Even in the model correlations remain significant after proximity and rank have been partialled out [Hemelrijk & Puga-Gonzalez, 2012]. Only when we omit these variables from the model in a different way, by making individuals interact with randomly chosen partners or by shuffling ranks among individuals every interaction, these correlations disappear [Hemelrijk & Puga-Gonzalez, 2012]. Hence, because partialling out is insufficient to eliminate the effects of proximity and rank in the model, previous analyses of empirical data may have also underestimated these effects as well.

"Calculated reciprocity" [Brosnan & de Waal, 2006] and "emotional bookkeeping" [Schino & Aureli, 2009] are two alternative mechanisms that have been suggested to underlie patterns of reciprocation and interchange of grooming and support in primate societies. However, there are several reasons why we think the distribution of contra-intervention is unlikely to be driven by these mechanisms in our study group. "Calculated reciprocity" suggests that individuals keep records of the number of acts given and received and that they adjust their behavior to pay back social partners

TABLE VI. TauKr Correlations Between Grooming, Aggression, and Opposition in Adult Female Bonnet Macaques When Partialling Out Rank of the Partner and Proximity

		Rank partialled out	Proximity partialled out
TauKr matrix correlations between	$TauKr_{xy}$ (*P*-value)	$TauKr_{xyz}$ (*P*-value)	$TauKr_{xyz}$ (*P*-value)
(1) Opposition given and aggression given	0.59 (0.000)	0.57 (0.000)	0.59 (0.000)
(2) Received opposition and received aggression	0.53 (0.000)	0.51 (0.000)	0.53 (0.000)
(3) Received aggression and grooming given	0.20 (0.002)	0.16 (0.022)	0.18 (0.012)
(4) Received opposition and grooming given	0.28 (0.000)	0.24 (0.001)	0.28 (0.001)
(5) Aggression given and received grooming	0.28 (0.000)	0.23 (0.001)	0.28 (0.000)
(6) Opposition given and received grooming	0.33 (0.000)	0.32 (0.000)	0.34 (0.001)

The $TauKr_{xy}$ and $TauKr_{xyz}$ coefficients and *P*-values are shown.

[de Waal & Brosnan, 2006; de Waal & Luttrell, 1988]. Thus, "calculated reciprocity" assumes an intentional interchange of services and favors among individuals and within such a framework individuals are not expected to interchange a beneficial act (grooming) for a harmful act (contra-intervention). Further, limitations in long-term memory make calculated reciprocity difficult even for humans [Stevens & Hauser, 2004; Stevens et al., 2011]; and studies investigating reciprocity and interchange in the short-term have found no conclusive evidence. Studies on Japanese macaques found no evidence that the receipt of grooming increased the short-term probability of giving back support or grooming [Schino et al., 2007, 2009]. In experiments with chimpanzees (*Pan troglodytes*), individuals fail to provide more food to partners from whom they received food previously [Brosnan et al., 2009], and male chimpanzees sharing meat with estrous females did not increase their mating probability in the short- or long-term [Gilby et al., 2010; Hemelrijk et al., 1992, 1999; Meier et al., 2000]. Similarly, in the GrooFiWorld model reciprocity of support is not the result of immediate exchange because reciprocity remains significant even after the cases of immediate exchange are excluded. In the model reciprocation and interchange result from rank and spatial positioning [Hemelrijk & Puga-Gonzalez, 2012].

Following the initial idea by de Waal [2000] on "attitudinal reciprocity," Schino & Aureli [2009] suggested "emotional bookkeeping" as an alternative to "calculated reciprocity." According to "emotional bookkeeping," the behavior of an individual toward another depends on the emotion associated with that specific partner; where emotions are considered to be influenced by past social interactions. Thus, the receipt of positive social interactions from a specific partner (e.g. receipt of grooming or support) strengthens the positive emotion associated with that partner. This positive emotion subsequently motivates the individual to reciprocate or interchange social services with it [Schino & Aureli, 2009]. The finding that female bonnet macaques interchange grooming for contra-intervention is not consistent with "emotional bookkeeping." Instead, the frequent receipt of dyadic aggression and contra-intervention should produce a negative emotion associated with that partner and thus reduce the interchange of social services.

In our study female bonnet macaques did not reciprocate support or interchange grooming for support (Table III). This result was unexpected according to Seyfarth's model of grooming for support [Seyfarth, 1977], to the biological market theory [Henzi & Barrett, 1999; Nöe & Hammerstein, 1994], and to what has been reported in some primate studies [Hemelrijk & Puga-Gonzalez, 2012; Schino, 2007]. The absence of reciprocation and interchange of grooming and support in our group of bonnet macaques may be due to the fact that support was not significantly correlated with dominance rank (Table IV). Instead, we found a strong association between contra-intervention and dominance rank (Table IV). This suggests that in this group third-party aggression is regulated by the identity of the individual to whom contra-intervention is directed rather than the identity of the individual supported. Indeed, in most cases of third-party aggression, the victim of aggression was lower ranking than the intervening female. From the 80 acts of contra-intervention, in 77 cases (96%) the intervening female directed contra-intervention toward a lower ranking individual.

The GrooFiWorld model predicts an effect of dominance rank on the distribution of social behavior only in groups with steep dominance hierarchies [Hemelrijk & Puga-Gonzalez, 2012]. We have previously reported that our study group of bonnet macaques exhibits a steep dominance hierarchy, namely a David's score of 0.64, which is similar to that found in other macaque species with an intolerant dominance style [Balasubramaniam et al., 2012]. This result is consistent with our current findings that the distribution of grooming and aggression in female bonnet macaques is characteristic of intolerant social groups. Similarly, Silk [1982] showed that female bonnet macaques groomed higher ranking females more frequently than those of lower rank and that the rate of grooming among females of similar rank was higher than that among those of distant ranks. In contrast, bonnet macaques have shown a tolerant dominance style on other traits such as reconciliation, kin-based social interactions, female acquisition of rank, infant handling and male emigration [Thierry 2000; Thierry et al., 2004]. For example, we have shown that the conciliatory tendency for females in our study group was 39.1% [Cooper et al., 2007], and thus, within the range described for tolerant macaque species [Thierry 2000; Thierry et al., 2004].

While much theoretical research has focused on the evolutionary mechanism underlying the evolution of reciprocation and interchange of social services, much less is known about the proximate mechanisms. The GrooFiWorld model was built with the goal of shedding light on proximate mechanisms, and it proposes a simple proximity-based mechanism which may have promoted reciprocation and interchange of social services early in the evolution of group-living primates. Whether this mechanism insures the evolutionary stability of reciprocation and interchange, or whether later in evolution other mechanisms may have evolved to insure its stability, is beyond the scope of our model.

In the present study we show that patterns of aggressive and affiliative behavior in female bonnet macaques are consistent with predictions derived

from the GrooFiWorld model. Importantly, females interchanged grooming and contra-intervention, as well as grooming and aggression, which suggests that the distribution of contra-intervention is determined by rank and the social-spatial structure in primate societies.

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